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A review of the volvatory Polydesmida, with special reference to the patterns of volvation (Diplopoda)

by

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ABSTRACT

The volvatory, or 'oniscoid' Polydesmida are reviewed at the family level, with descriptions of their volvation patterns, and diagnostic accounts for the following nine groups involved: Ammodesmidae, Campodesmidae, Cyrtodesmidae, Doratodesmidae, Dorsoporidae, Oniscodesmidae, Sphaeriodesmidae, *Hyperothrix* Attems, 1900 (?Pyrgodesmidae), and *Asphalidesmus* Silvestri, 1910 (Dalodesmoidea). These patterns, although rather characteristic at the generic level, are now known to vary within, as well as between families; this perception plus some new observations allow refinements to the existing classification of Polydesmida.

INTRODUCTION

Volvation, or conglobation among Diplopoda is rather widespread, and is presumed to be an adaptation for protection against predators and desiccation (Lawrence 1953; Simonsen 1990), particularly in miniature diplopods likely to exhibit mimesis as well. Millipedes capable of rolling up into a tight ball are represented by the orders Sphaerotheriida and Glomerida, which comprise the superorder Oniscomorpha of the subclass Pentazonia. These diplopods are often referred to as 'pill millipedes'. Species of the oligotypic South African genus *Cylichnogaster* Verhoeff, 1937 (order Polyzoniida) and several lineages of the order Polydesmida can form a compact disc or coil when rolled up. Such volvatory species are often termed 'oniscoid millipedes'. Both oniscomorph and 'oniscoid' diplopods are so named to emphasise their strong overall resemblance to certain 'armadilloid' woodlice (suborder Oniscidea, order Isopoda, class Crustacea), though, paradoxically, species of the 'patronym' woodlouse genus *Oniscus* Linn. are incapable of volvation (cf. Schubart 1934). Hence quotation marks are used here to designate 'oniscoid' Polydesmida.

The bulk of Diplopoda, largely representatives of the infraclass Helminthomorpha, can only spiral when disturbed, the coil if any being relatively loose and incomplete, leaving parts of the head, antennae and legs exposed (Lawrence 1953). Some callipodidans, e.g. *Abacion* Rafinesque, 1820, and many other cylindrical millipedes can roll up into a one-plane (= flat) spiral of several complete turns (Shelley 1990), but no spiral, however tight, can be compared with true conglobation.

Hence volvation appears to occur in four of the 15 or 16 orders, and three of the subclasses accepted in Diplopoda at present (Hoffman 1980 1982*b*; Shelley 2003: 21). This alone strongly suggests that numerous parallelisms have occurred among volvatory millipedes. The same is generally true of the phylum Arthropoda as a whole, where volvatory members are known to be scattered throughout the Crustacea, Myriapoda, Arachnida and Insecta (Lawrence 1953).

In Diplopoda, the most conspicuous modifications to complete conglobation normally involve tergum 2 or, more rarely, either only tergum 3 or both terga 3 and 4 being strongly enlarged while the collum is usually relatively small, not covering the head from above. These developments are associated with a broadened body; the dorsum is highly convex, nearly all or even all postcollar paraterga are strongly deflexed, often subvertical, and usually produced ventrad beyond the normally very narrow sterna which barely separate the coxae. The antennae are usually short, more rarely long and slender. Legs can also be long and slender but are usually relatively short, normally not extending beyond the lateral edges of the paraterga. The telson (= anal segment) is either voluminous, forming a prominent hemispherical caudal shield called the pygidium (Oniscomorpha, Fig. 1) or relatively small, sometimes reduced and almost to fully concealed from above under the paraterga of the penultimate body segment (certain Polydesmida). The body is invariably relatively short; even in the colobognathan genus *Cylichnogaster* the number of body segments only slightly exceeds 20, that is, close to that of Polydesmida.

The present paper focuses on volvatory Polydesmida, with consideration of the patterns of volvation and some new observations in the fields of comparative and functional morphology, to shed additional light on the relations between the various polydesmidan lineages. While the family status of the remaining volvatory Diplopoda families is virtually undisputed (Hoffman 1980), the classification of Polydesmida is still an arena of debate.

RIVAL CLASSIFICATIONS

As a recent historical account of the classification of ‘oniscoid’ Polydesmida is available (Hoffman 1990), it seems sufficient to reiterate here that some 60 years ago both Attems (1940) and Verhoeff (1941) grouped all such forms into the two families Sphaeriodesmidae and Oniscodesmidae. Verhoeff (1941 1942) lumped all volvatory Polydesmida into a single suborder, Sphaeriosomita, a completely unjustified, hopelessly heterogeneous taxon based solely on the animal’s ability to roll up or coil (e.g. Hoffman 1977). Currently species of the order Polydesmida, essentially capable of volvation, are accepted as being distributed between as many as eight families (Ammodesmidae, Campodesmidae, Cyrtodesmidae, Doratodesmidae, Dorsoporidae, Oniscodesmidae, Pyrgodesmidae, and Sphaeriodesmidae) assigned to four different superfamilies and two suborders. However, certain interrelations and assignments are rather unclear and need to be refined.

Hoffman’s (1980 1982*b*) classification, with all subsequent modifications (Hoffman 1998; Hoffman *et al.* 2002), recognises the following arrangement (families containing volvatory/oniscoid species in bold):

- Order Polydesmida
- Suborder Paradoxosomatidea
    - Family Paradoxosomatidae
- Suborder Chelodesmidea
    - Superfamily Chelodesmoidea
        - Family Chelodesmidae

- Superfamily Xystodesmoidea
    - Family Xystodesmidae
    - Family Eurymerodesmidae
    - Family Gomphodesmidae
    - Family Oxydesmidae
    - Family Euryuridae
- Superfamily Sphaeriodesmoidea
    - Family **Sphaeriodesmidae**
    - Family Holistophallidae
    - Family **Campodesmidae**
- Superfamily Platyrhacoidea
    - Family Platyrhacidae
    - Family Aphelidesmidae
- Superfamily Rhachodesmoidea
    - Family Rhachodesmidae
    - Family Tridontomidae

Suborder Polydesmidea

- Superfamily Polydesmoidea
    - Family Polydesmidae
    - Family **Doratodesmidae**
    - Family Haplodesmidae
    - Family Cryptodesmidae
    - Family Opisotretidae
- Superfamily Trichopolydesmoidea
    - Family Trichopolydesmidae
    - Family Macrosternodesmidae
    - Family Nearctodesmidae
    - Family Fuhrmannodesmidae
- Superfamily Pyrgodesmoidea
    - Family **Pyrgodesmidae**
    - Family **Cyrtodesmidae**
- Superfamily Oniscodesmoidea
    - Family **Oniscodesmidae**
    - Family **Dorsoporidae**
    - Family **Ammodesmidae**

Suborder Dalodesmidea

- Family Dalodesmidae
- Family Vaalogonopodidae

Based on a cladistic analysis, Simonsen (1990) arrived at the following classification of the suborder Polydesmidea:

Infraorder Oniscodesmoides

- Superfamily Oniscodesmoidea
    - Family **Oniscodesmidae**
- Superfamily Pyrgodesmoidea
    - Family **Cyrtodesmidae**

- Family **Pyrgodesmidae**
- Family **Ammodesmidae**

Infraorder Polydesmoides
- Superfamily Trichopolydesmoidea
  - Family Fuhrmannodesmidae
  - Family Trichopolydesmidae
  - Family Macrosternodesmidae
- Superfamily Opisotretoidea
  - Family Opisotretidae
- Superfamily Haplodesmoidea
  - Family Haplodesmidae
  - Family **Doratodesmidae**
- Superfamily Polydesmoidea
  - Family Cryptodesmidae
  - Family Polydesmidae
  - Family Dalodesmidae

In the latter classification, the Dorsoporidae has been merged with the Oniscodesmidae. In addition to some further new combinations, status changes and synonymies introduced by Simonsen (1990), but irrelevant to the present paper, the family Ammodesmidae has been reassigned to the superfamily Pyrgodesmoidea, while the remaining volvatory families Sphaeriodesmidae and Campodesmidae have been left intact within the Chelodesmidea, but without a superfamily placement. Besides this, the suborder Dalodesmidea has been dismissed, and the single family Dalodesmidae placed inside Polydesmidea.

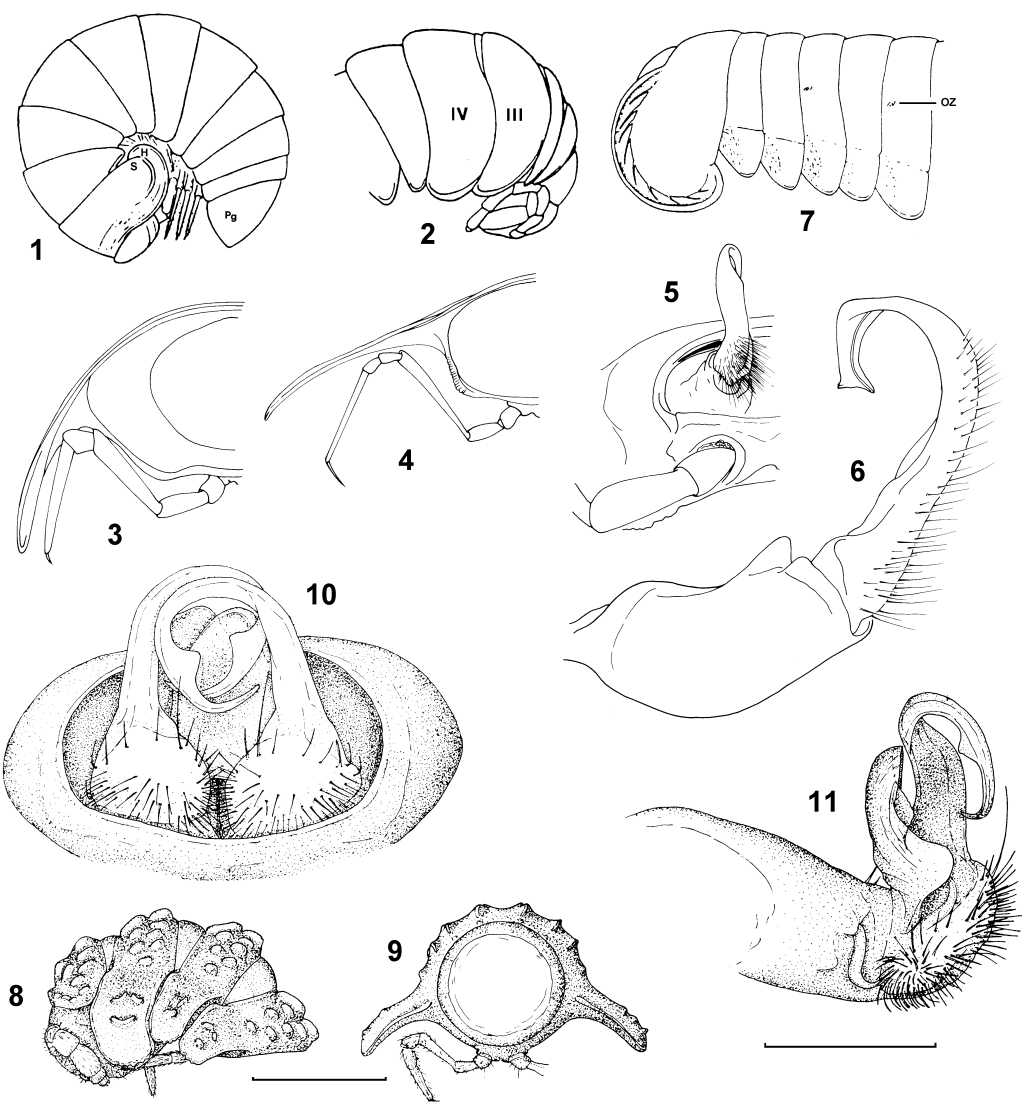
If these classifications are taken as reflecting true relationships (= phylogeny), they both require at least two independent origins of volvation within Polydesmidea alone.

VOLVATION PATTERNS AND DESCRIPTIVE ACCOUNTS

Very little attention appears to have been paid to patterns of volvation in the various ‘oniscoid’ Polydesmida. Below is a concise presentation of the patterns in each of the volvatory polydesmidan families as based, wherever possible, on a study of pertinent material. In the few cases when no such material was available, only literature data have been used.

The **Sphaeriodesmidae** is the only family in which either tergum 3 or both terga 3 and 4 can be enlarged (Fig. 2). Conglobation implies that the lateralmost, narrowed parts of the paraterga of several segments both subsequent to and in front of the broadest segment (3 or 4) are hidden under the latter. Starting from body segment 4 or 5, the lateral, subacuminate end of each subsequent paratergum is hidden under and behind the previous one, thus displaying an overlap pattern which can be termed typical. The telson usually is flattened, with a fully exposed, broad, plate-like epiproct; during complete volvation of the animal it is tightly oppressed to the dorsal side of body segment 5 or 6.

This family is characterised, among other things, by long and slender antennae and legs (Figs 3, 4); antennomere 5 is longer and often larger than antennomere 6; the paraterga are very prominent and relatively simple (Fig. 3), the dorsum is smooth to



Figs 1–11. Structure of some 'oniscoid' Diplopoda. 1: *Glomeroides* sp. (Glomeridae, Glomerida), lateral view (S = schism, or suture; H = hyposchism, or field below schism; Pg = pygidium). 2 & 3. *Sphaeriodesmus* sp. (Sphaeriodesmidae, Polydesmida), anterior body portion (III and IV = segment numbers) and cross-section of a midbody segment, lateral and caudal views, respectively. 4–6: *Proeilodesmus mecistonyx* Hoffman, 1990 (Sphaeriodesmidae, Polydesmida), cross-section of a midbody segment, right half of male body segment 7, and right gonopod, caudal, ventral, and lateral views, respectively. 7. *Dorsoporus barroensis* Loomis, 1958 (Dorsoporidae, Polydesmida), anterior body portion, lateral view (OZ = ozopore). 8–11. *Campodesmus dilobatus* (Schiøtz, 1966) (Campodesmidae, Polydesmida), anterior body portion, cross-section of a midbody segment, gonopods *in situ*, and left gonopod, lateral, front, ventral, and mesal views, respectively. [1 & 2 after Hoffman *et al.* (2002) (reprinted courtesy of Pensoft Publishers); 3–6 after Hoffman (1990) (reprinted courtesy of the Swiss Zoological Society); 7 after Loomis (1958) (reprinted courtesy of the Journal of the Washington Academy of Sciences); 8–11 after Schiøtz (1966) (reprinted courtesy of the Danish Natural History Society). Scale bars 0.5 mm (10 & 11) and 2.0 mm (8 & 9), others reproduced not to scale.]

roughly tuberculate, the ozopores are very small to missing; the tergal limbus is evident but nearly smooth; the gonopod aperture is transversely oval and modest in size; the gonopods are simple to relatively complex (Figs 5, 6), highly variable but subcylindrical coxae nearly always have a sternal rudiment, the cannula is normal to hypertrophied basally. The body is usually medium-sized and 15–35 mm long. Further structural details can be found in Hoffman (1982*b* 1990) and Simonsen (1990). Nearly completely volvated members of the subfamily Desmoninae are depicted in Shelley (2000).

Sphaeriodesmids currently comprise 14–15 genera and about 90 described species, but the actual diversity exceeds 200 species (Hoffman 1990; Hoffman *et al.* 2002). The family is endemic to Central America and the Greater Antilles, ranging from between north of Panama to Missouri and Kentucky in the USA.

What seems particularly remarkable is that this family still comprises at least one genus and species, the cave-dwelling Mexican *Proeilodesmus mecistonyx* Hoffman, 1990, that is apparently not capable of volvation (cp. Figs 3 & 4). Most of the characters of this creature seem plesiomorphic and suggest a link between a presumed flat-bodied chelodesmidean ancestor and the remaining, convex, truly volvatory members of the family (Hoffman 1990).

In Sphaeriodesminae, the prozona are reduced to virtually absent ventrally, paralleling the situation in Oniscomorpha, but in Desmoninae, a group of Sphaeriodesmidae, the prozona are about the same length all the way around. Desmonines thus resemble a flattened oblate spheroid (= disc) rather than a true sphere as in species of *Sphaeriodesmus* Peters, 1864. Being about 15 mm wide, *S. mexicanus* (De Saussure, 1859), from Mexico, is probably the largest polydesmidan currently known to roll up.

The phylogenetic relations of the Sphaeriodesmidae seem particularly close to the Holistophallidae, a small group endemic to Central America and incapable of volvation (Hoffman 1980 1982*b*; Hoffman *et al*. 2002).

In all other 'oniscoid' polydesmidan families, it is only the second tergum that is more or less enlarged and adapted for volvation. In addition, the antennae, and usually the legs, are relatively short; the latter are sometimes separated to a varying degree, even on the same body segment (Fig. 42).

The **Campodesmidae** is monogeneric, with all 7–8 species of the single accepted genus *Campodesmus* Cook, 1896, from tropical West Africa. These species are medium-sized (28–38 mm long), dark, with more or less strongly tuberculate metaterga and modestly deflexed paraterga, so that the usually dentate lateral edge of paraterga is nearly at the same level as the sterna (Schiøtz 1966). The modestly enlarged paratergum 2 is devoid of any special structures except a rather shallow caudolateral emargination for the accomodation of the anterolateral parts of the moderately deflexed subsequent paraterga. This structure suggests incomplete or imperfect volvation (Figs 8, 9), and also implies a typical pattern of overlap. Direct observations confirm enrolment into a partial coil, a flattened oblate spheroid, rather than a true ball (Hoffman 1982*b*).

The telson is 'polydesmoid' in the sense that it is typical of non-volvatory Polydesmida (cf. Hoffman 1982*b*), i.e. fully exposed from above, with normal, large paraprocts (= anal valves) and a considerable hypoproct (= subanal scale), though the epiproct is strongly flattened and somewhat tuberculate. Nothing can be gained from available literature, as to opposite which body segment the telson of a completely coiled animal might rest. Yet, during the volvation, which can certainly be regarded as imperfect, especially when the collum and subsequent terga are armed with conspicuous tubercles, the flattened epiproct may be assumed to reach only as far as the collum or at most another of the few anteriormost terga.

Among the characters of Campodesmidae that attest to the group's chelodesmidean stock, the gonopod structure is the most basic (Hoffman 1980 1982*b*). This involves a large, transversely oval gonopod aperture containing elongate, subcylindrical coxae, loosely connected by a membrane, each coxa with a normal cannula; an elongate telopodite coiled distally, with a more or less strong protuberance medially at the base of the femorite (Figs 10, 11).

The pore formula is incomplete, with ozopores only present on paraterga 5 and 7. The rough metaterga are often covered with a soil crust, and the cuticle is finely granular. Antennomere 5 is longer than antennomere 6. The male coxa 2 bears a considerable distomedian process carrying the gonopore orifice; this trait is generally characteristic of the suborder Chelodesmidea. Further structural details of the family can be found in Schiøtz (1966) and Hoffman (1982*b*).

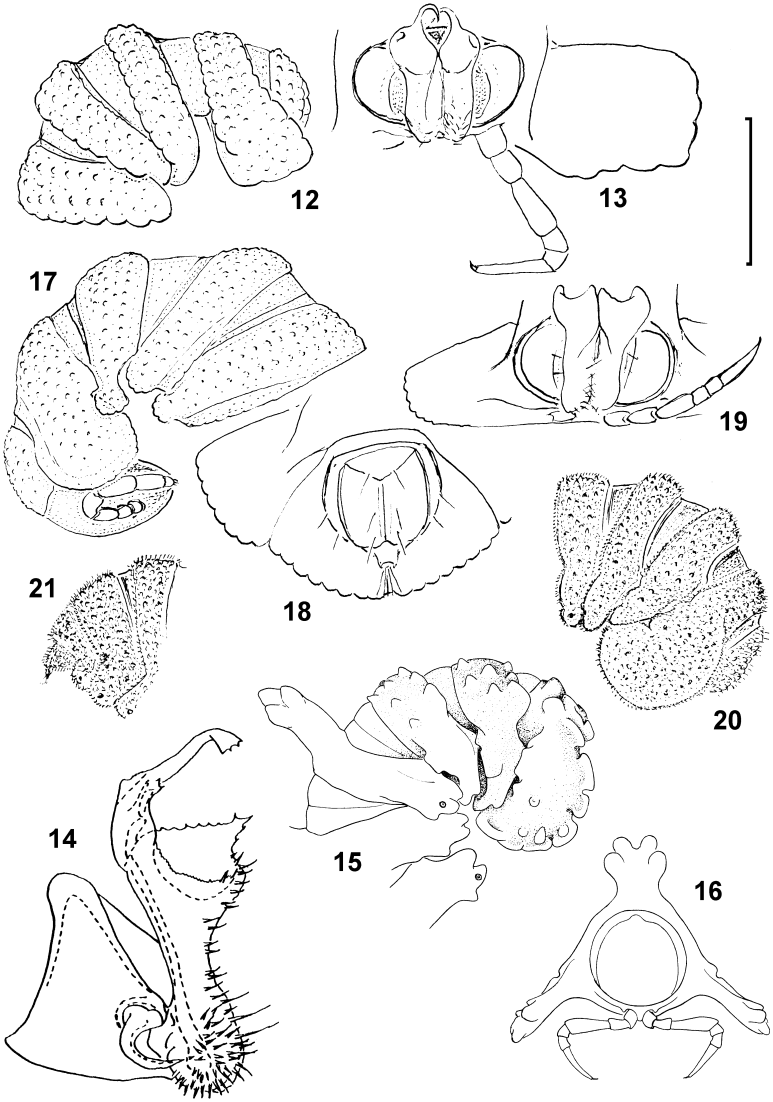
Interestingly, tergum 2 in some congeners seems somewhat more incrassate than in others, e.g. *Campodesmus dilobatus* (Schiøtz, 1966) (Fig. 8).

The affinities of Campodesmidae within the Chelodesmidea are not entirely clear. According to Hoffman (1982*b*), not only Sphaeriodesmidae and Holistophallidae (cf. Hoffman 1980), but also Campodesmidae can be assigned to the superfamily Sphaeriodesmoidea.

The **Doratodesmidae** is a relatively small family currently comprising 13 largely monobasic genera (Zhang & Wang 1993). The volvation pattern is much more advanced, and this is apparently related to the particularly enlarged paraterga 2. A narrow flange or ledge (= hyposchism, as accepted in Oniscomorpha, Fig. 1, H) near the rear margin of the broadest paratergum 2, beneath and behind a series of more or less tuberculiform lobules (= suture, = schism, Fig. 1, S), appears specially designed to accommodate paratergum 3. The latter, in turn, shows a similar but even narrower flange for the anterolateral part of paratergum 4 to hinge into. The same concerns paratergum 4 and its hyposchism, which is specially designed for the receipt of the anterolateral portion of paratergum 5. Then the pattern changes so that the anterolateral portion of each paratergum subsequent to the fifth is placed beneath the caudal margin of the previous paratergum (Figs 12, 15). In other words, there is no hyposchism on the paraterga of body segments 5–18(19), hence the overlap is switched to typical, starting from body segment 5. Conglobation is tight and the coil is definitely complete.

The telson is normal but is usually tuberculate, 'polydesmoid', and with a fully exposed and conspicuous epiproct. During complete volvation of the animal the telson is tightly oppressed to the dorsal side of body segment 4 (when the following metaterga are provided with larger mid-dorsal protuberances, Figs 15, 16), or 5 or 6 (when all metaterga are devoid of stronger mid-dorsal processes, Fig. 12).

This family is characterised, amongst other things, by the prominent and relatively complex paraterga. The latter are always more or less strongly lobulated to incised at the lateral margin (Figs 12, 15); the dorsum is more or less roughly tuberculate, and certain metaterga in some species have particularly prominent mid-dorsal tubercles or crests (Figs 15, 16). The ozopores are very small to missing; the gonopod aperture is transversely oval and large (Fig. 13); the gonopods (Figs 13, 14) vary from simple to



Figs 12–21. Structure of some ‘oniscoid’ Polydesmida. 12–14. Crenatidorsus grandifoliatus Zhang & Wang, 1993 (Doratodesmidae), anterior body portion, left half of body segment 7, and left gonopod, lateral, ventral, and mesal views, respectively. 15 & 16. *Ascetophacus macclurei* Hoffman, 1977 (Doratodesmidae), anterior body portion and cross-section of a midbody segment, lateral and caudal views, respectively. 17–19. *Crypturodesmus* sp. (Oniscodesmidae), anterior body portion, right half of body segment 7, and caudal body end, lateral, ventral, and ventral views, respectively. 20 & 21: *Cyrtodesmus* sp. (Cyrtodesmidae), anterior and posterior body portions, lateral view. [12 & 13, original, male from China, Yunnan, Mengzi County, Cave Chi Be Yi Dong, 07.01.1989, leg. P. Beron (Sofia Museum); 14 after Zhang & Wang (1993); 15 & 16 after Hoffman (1977) (reprinted courtesy of Bishop Museum Press); 17–19, original, male from Brazil, Mato Grosso do Sul, Bonito, Gruto da Carneiro, 6–8.04.1998, leg. R. Pinto-da-Rocha & G. Sessegolo (São Paulo Museum); 20 & 21, original, male from Peru, Prov. Loreto, island at mouth of Yanayacu River, *ca* 65 km downstream Rio Amazonas from Iquitos, whitewater inundation forest, rotton wood, 22.03.1998, leg. J. Adis, S. Golovatch & A. Mármol (Moscow Museum). Scale bar 1.0 mm (12 & 13) and 2.0 mm (17–21), others reproduced not to scale.]

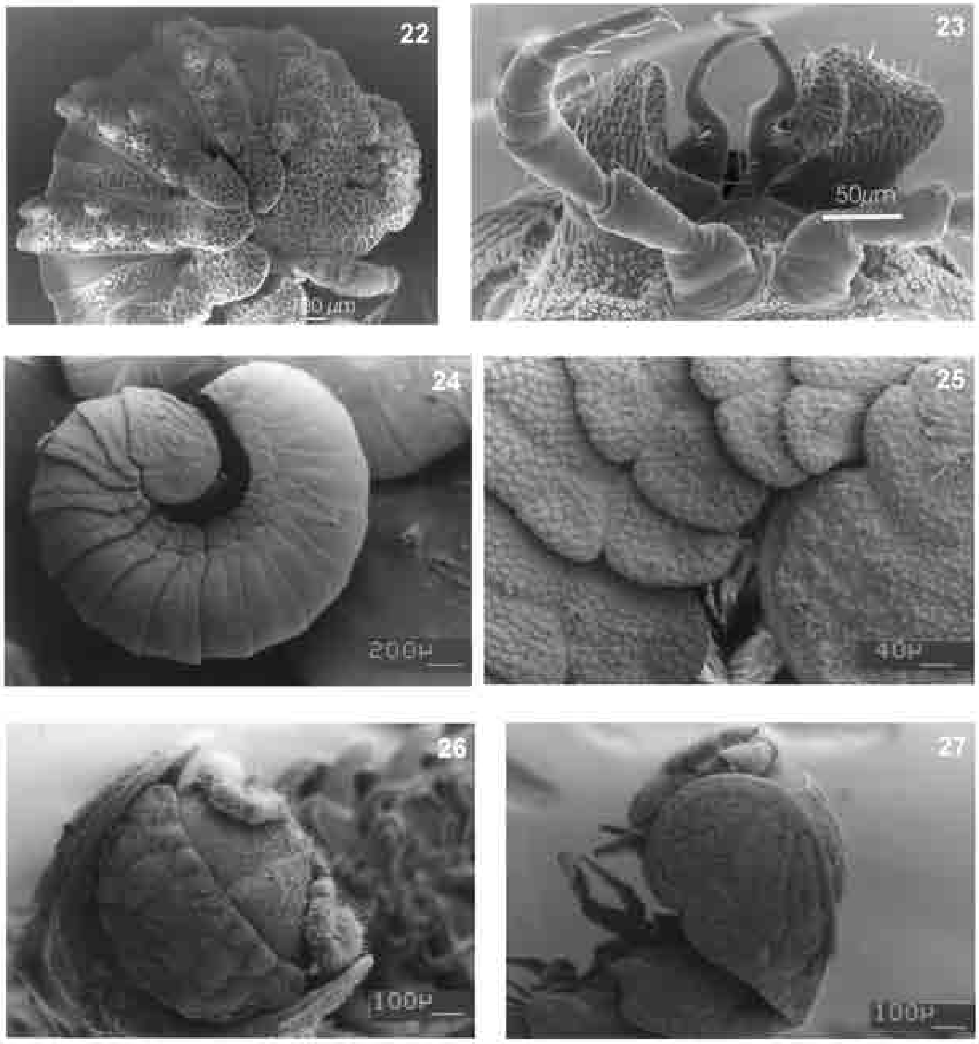
relatively complex, the telopodite is invariably elongate, the prefemoral portion is small, the coxae are subtriangular and fully fused along the midline, and each has a normal cannula; antennomere 6 is longer and larger than antennomere 5; the body is usually relatively small, 6–15 mm long and the limbus is present and dentate-spatulate. Further structural details can be found in Hoffman (1977 1982*a* 1982*b* 1990) and Simonsen (1990). Certain observations of the volvation pattern are provided by Hoffman (1977). The family is endemic to south-east Asia (with Yunnan, China and southern Japan being the northernmost records), the Indo-Australian archipelago and New Guinea.

Following both Hoffman (1980 1982*b*) and Simonsen (1990), based on the gonopod structure, the relationships of Doratodesmidae are deemed particularly close to the Indo-Australian family Haplodesmidae, a small group often displaying enlarged paraterga 2, but not capable of volvation.

The **Oniscodesmidae** as currently defined (Hoffman 1980 1982*b*; Simonsen 1990) contains eight or nine nominal genera, all in South and/or Central America. Most genera are monobasic, only the southernmost *Crypturodesmus* Silvestri, 1897 (Brazil and Argentina) is relatively species-rich. The conglobation pattern is similar to the previous case, but it varies even between genera. The spatulate, rounded, strongly enlarged lateral pieces of paraterga 2, sometimes (*Detodesmus* Cook, 1896) have a distinctly elevated anterior margin and a narrowed and flattened dorsum (the latter often angular at the bases of paraterga, Figs 26, 27), and they always possess a narrow hyposchism behind a lobuliform schism. This is small in *Amphitomeus* Verhoeff, 1942 (Figs 24, 25), with a typical overlap of the subsequent paraterga. During complete volvation the lateral ends of several paraterga subsequent to the second, rest over a narrow rim of the latter (cf. Golovatch *et al*. 2002). In *Crypturodesmus* (Fig. 17), the caudolateral margin of paratergum 3 is very strongly emarginate or sinuate for the accommodation of the anterolateral portion of paratergum 4, but posterior to this the overlap is typical, with the lateral ends of several paraterga subsequent to the fourth likewise resting over a narrow rim of paratergum 2.

The telson tends to become reduced. In *Amphitomeus* (Figs 28–30), the only 19-segmented oniscodesmid genus, the telson is still evidently exposed in dorsal view (Figs 29, 31), although the epiproct is short and strongly flattened (Fig. 30) (cf. Golovatch *et al*. 2002). In *Crypturodesmus*, the telson in dorsal aspect is completely hidden under the medially fused paraterga of the penultimate body segment (Fig. 18). In both cases, in a completely enrolled animal, a pygidium-like caudal body end rests tightly oppressed to the region of segments 2–5.

The family is characterised by small to medium-sized species (3–22 mm long). The tergal surface is usually polished, but sometimes finely microgranular or scaly (*Amphitomeus*, Fig. 25); the metaterga are often (Fig. 17) but not always tuberculate, or infrequently areate along the rear tergal margin behind a transverse sulcus or depression (*Oniscodesmus*, *Detodesmus* and some others), and only rarely almost smooth (*Amphitomeus*). The paraterga are sometimes lobulate or crenulate at the lateral edge (*Crypturodesmus*, Figs 18, 19), and they are rarely incised at the base both anteriorly and, especially deeply, posteriorly (*Amphitomeus*, Figs 24, 25). The tergal limbus is (nearly) missing; antennomere 5 is longer and larger than antennomere 6; the pore formula is usually complete and normal, but the ozopores are small, and open flush on the surface near the base of the respective paraterga and more rarely the ozopores are



Figs 22–27. Scanning electron micrographs of some ‘oniscoid’ Polydesmida. 22 & 23. *Elassystremma* sp. (Ammodesmidae), anterior body portion and ventral side of male body segment 7, lateral and subcaudal views, respectively. 24–27. *Amphitomeus attemsi* (Schubart, 1934) (Oniscodesmidae), entire animal, paraterga 2–7, and anterior body end, lateral, lateral, subdorsal, and lateral views, respectively. [22 & 23 after Van den Spiegel (in prep.) (reprinted courtesy of the Royal Museum for Central Africa); 24–27 after Golovatch *et al.* (2002) (reprinted courtesy of *Arthropoda Selecta*).]

absent altogether (*Crypturodesmus*); the legs are relatively slender; the gonopod aperture is transversely oval to subcordate (Fig. 19) and relatively large; the gonopod coxae are relatively small, subglobose, fused medially, largely sunken inside the aperture, and with normal cannulae; the telopodite is suberect, and the setose prefemoral part is always substantial (Figs 19, 32).

This family is deemed to be particularly closely related to the Dorsoporidae (Hoffman 1980 1982*b*), while Simonsen (1990) has even merged both into a single family

Oniscodesmidae. For practical reasons, however, *Dorsoporus* Loomis, 1958 does deserve a separate treatment.

The **Dorsoporidae** is a monotypic taxon, with *Dorsoporus barroensis* Loomis, 1958, from Panama, characterised by the ozopores located on small knobs above the base of the paraterga (Fig. 7, OZ) and, somewhat like in *Amphitomeus* (Fig. 25), by a longitudinal sulcus setting off the posterior half of the paraterga from the rest of the metaterga. The body segments are smooth, polished, the telson is somewhat reduced, the epiproct is flat, rounded at the caudal edge, yet quite visible in dorsal view, while the legs are rather long and slender (Loomis 1958). As no male material of *Dorsoporus* has hitherto become available, it appears impossible to add anything to Hoffman *et al.* (2002), who still provisionally keep this family separate. The volvation pattern distinctly implies one of a typical oniscodesmid like *Amphitomeus,* with a narrow hyposchism of paratergum 2 apparently receiving the lateral ends of several following paraterga which apparently show a typical overlap (Fig. 7). A possible reallocation of *Dorsoporus* within the Sphaeriodesmoidea, as once suggested by Hoffman (1982*b*), is thus unlikely.

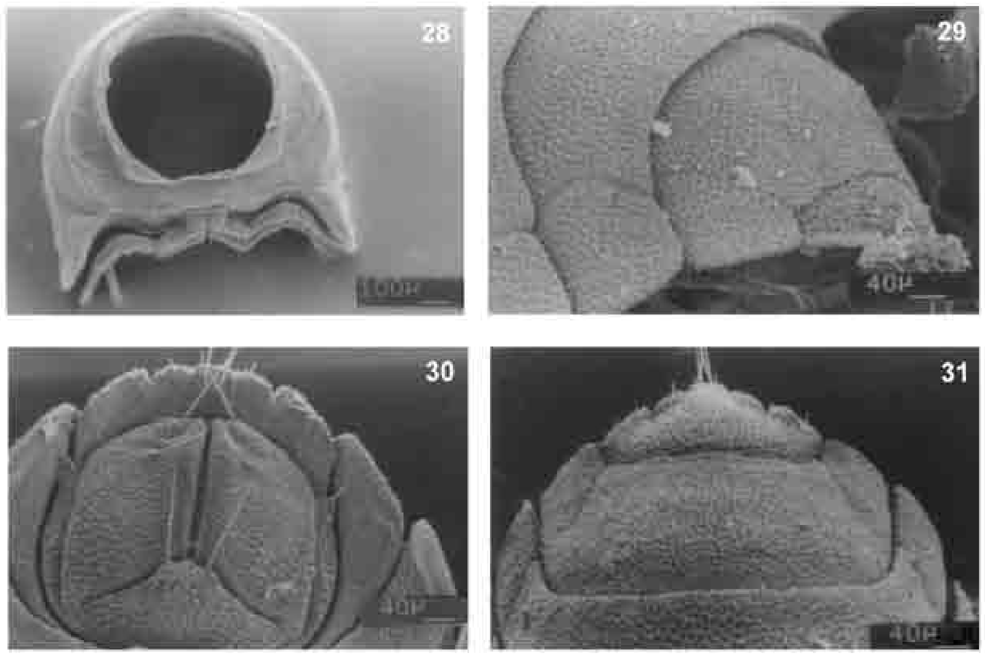
The **Ammodesmidae** is an oligotypic family with three genera and several species in tropical Africa (Hoffman & Howell 1981; Van den Spiegel, in prep.). They are all so minute (2–5 mm long) that, when coiled and dusted with earth, these animals resemble a grain of sand (Cook 1896). The conglobation pattern in the East African *Elassystremma* Hoffman & Howell, 1981 appears to be very much like in Doratodesmidae, but the overlap only becomes typical from paratergum 4 onwards (Figs 22, 33).

The telson is likewise normal, ‘polydesmoid’, and evident from above. The epiproct is flattened, conspicuous, sometimes tuberculate (Fig. 33), and during complete volvation of the animal it is tightly oppressed to the dorsal side of body segment 5 or 6.

The body teguments are usually rough; the metaterga are more or less strongly tuberculate, and the paraterga are rounded laterally, usually somewhat incised or sinuate anteriorly and caudally at their base (Figs 22, 33); the ozopores are small, poorly visible, and they open flush on the surface of the paraterga below the caudobasal incision; the ozopore formula seems to be somewhat abbreviated: 5, 7, 9, 12, 15, 17–18(19) (Fig. 33), and sometimes ozopores seem to be missing; the tergal limbus is evident and is dentate; antennomere 5 is longer and larger than antennomere 6 (Fig. 22); the legs are rather slender but short (Fig. 23); the gonopod aperture is transversely oval and large; the gonocoxae are extremely large and subtriangular, with normal cannulae which are strongly exposed; the gonocoxae are fused and hollow medially and often enlarged laterally so that the more or less slender telopodites are nearly fully concealed inside the gonocoel (Figs 23, 34) (Hoffman & Howell 1981; Van den Spiegel, in prep.).

The only qualification to be noted here is that it still remains to be proven if both West African genera, *Ammodesmus* Cook, 1896 and *Cenchrodesmus* Cook, 1896, are indeed confamilial with *Elassystremma* (cf. Hoffman & Howell 1981).

The **Cyrtodesmidae** is yet another small family containing only three accepted genera, two of which are oligotypic (*Oncodesmella* Kraus, 1960, 2 species, and *Agnurodesmus* Silvestri, 1910, 4 species), and one which is rather more prolific (*Cyrtodesmus* Cook, 1896, about 25 species) (Golovatch 2001). The family occurs on the island of Tobago, Central America from Costa Rica southwards, and northern South America southwards to Amazonia.



Figs 28–31. Scanning electron micrographs of *Amphitomeus attemsi* (Schubart, 1934) (Oniscodesmidae), cross-section of a midbody segment and caudal body end, front, lateral, ventral, and dorsal views, respectively. [All after Golovatch *et al.* (2002) (reprinted courtesy of *Arthropoda Selecta*).]

Volvation is either imperfect (*Agnurodesmus*), this being testified by the relatively short paraterga being only slightly deflexed ventrad below the level of sterna, or complete (*Cyrtodesmus*, probably also *Oncodesmella*). In the former case, the pattern is much like in Campodesmidae, with a strongly enlarged paratergum 2 which is emarginate caudolaterally for the accommodation of the anterolateral protuberance of paratergum 3. The latter is also strongly emarginate caudolaterally. There is neither a schism nor a hyposchism on paratergum 2, but starting from paratergum 3 the overlap is typical. The only peculiarity is that the broadened, dentate or crenulate paraterga show a lunular flange anteriorly and a caudal protuberance caudolaterally, with the latter fitting in the former of the next paratergum during volvation (Fig. 37). In contrast, conglobation in *Cyrtodesmus* involves the development of a lobuliform schism and a narrow hyposchism in a typically roundly spatuliform paratergum 2, and of a subacuminate, not broadened, end of each subsequent paratergum (Fig. 20). The overlap is retained in the typical form. This condition strongly resembles that of *Amphitomeus* among Oniscodesmidae.

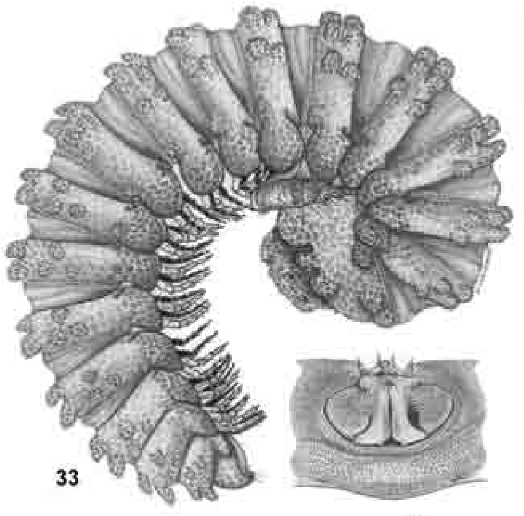
Also as in Oniscodesmidae, the telson in cyrtodesmids tends to be reduced, being fully concealed under the paraterga of the penultimate body segment in *Agnurodesmus* (Fig. 39). In a completely enrolled *Cyrtodesmus* species, the small, somewhat pygidium-like telson is fully exposed in dorsal view, the tip of the epiproct is nearly fully hidden underneath, and the entire caudal body end (Fig. 21) appears to rest on top of body segment 4. In *Agnurodesmus siolii* Golovatch, 2001, it is placed on top of metatergum 5 or 6.

The above progression is more or less paralleled by a trend towards the complication of gonopod structure, from the relatively small gonocoxae and strongly exposed telopodites in *Oncodesmella*, to the strongly enlarged coxae and shield-like structures protecting the remaining parts inside the gonocoel in *Agnurodesmus*. Based on structural details, the genus *Agnurodesmus* can soundly be considered as especially disjunct. This opinion agrees with biogeographical evidence as well (Golovatch 2001). Even though volvation in this genus appears incomplete, its pattern is unique among all 'oniscoid' Polydesmida.

Even amongst *Cyrtodesmus* species there is one, *C. bicolor* Loomis, 1964, from Panama, in which, due to the much smaller paratergal lobes of the second segment, only incomplete volvation can be suggested (Loomis 1964), i.e. a kind of 'plesiomorphic' status like that of *Proeilodesmus* as opposed to *Sphaeriodesmus* in Sphaeriodesmidae. Hoffman (1999) lists *C. bicolor* among Cyrtodesmidae of uncertain generic position.

Among the other traits characteristic of Cyrtodesmidae, the usually blackish to piceous teguments with contrastingly pinkish antennae deserve mention. The body is relatively small (5–20 mm long), the teguments are rough (Figs 20, 21, 37–40), the metaterga are always tuberculate and often setose; the epicranial region is granulorugose (Fig. 41), the limbus is crenulate/dentate; antennomere 5 is usually but not always longer and larger than antennomere 6 (Fig. 41); the pore formula is usually but not always normal; the legs are relatively short and stout (Fig. 42); and the solenomere is always branched (Figs 43, 44). Further characteristics can be found in Golovatch (2001). Many of the traits in Cyrtodesmidae, however, appear to be shared with the definitely closely related but very large and diverse family Pyrgodesmidae.

The monobasic genus ***Hyperothrix*** Attems, 1900, with the single small species *H. orophura* Attems, 1900, from a few of the larger granitic islands of the Seychelle Archipelago, has long attracted attention as another superficially 'oniscoid' polydesmidan still without clear family placement (Hoffman 1982*a*; Golovatch & Korsós 1992; Golovatch 2001). This genus and species has repeatedly been assigned to or compared with such different families as Oniscodesmidae, Pyrgodesmidae, Cyrtodesmidae or Doratodesmidae, with the latest return to Pyrgodesmidae on the basis of a typically pyrgodesmid-like tergal lobulation pattern and, above all, the gonopod conformation (Golovatch 2001). In *H. orophura*, in addition to the fairly detailed descriptions by Attems (1900 1940), the vertigial region of the head is granulorugose but not elevated; the collum is rather convex, somewhat enlarged, yet failing to cover the head from above (Fig. 35), and with a clearly elevated anterior rim showing an indistinct pattern of 6+6 lobulations. Tergum 2 is evidently, but not too dramatically, hypertrophied, with each of its paraterga deeply trilobate, andenlarged laterad (Fig. 35). The paraterga of body segments 3 and 4 are deeply bilobed, subsequent quadri- (pore-bearing segments) or trilobulate (poreless segments) laterally. The terga are generally very strongly convex but the paraterga are modestly broad, ending a little above the level of the sterna. The limbus is bacilliferous; the ozopores are normally located on low knobs and the pore formula is normal; the metatergal surface is rough, granular, very finely pilose, with the tuberculation rather poorly differentiated but the pattern typically pyrgodesmid, and this is especially evident toward the telson, which is fully concealed in dorsal



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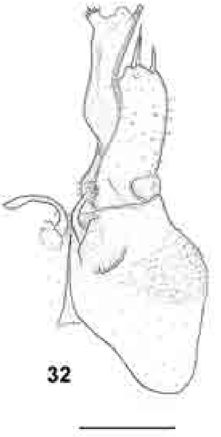

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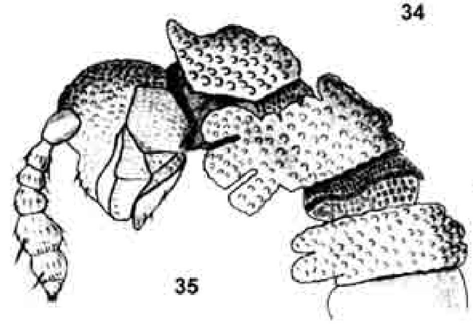

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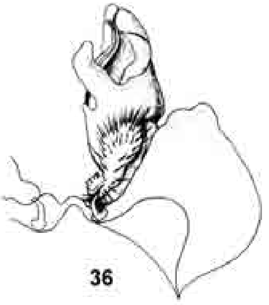

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Figs 32–36. Structure of some 'oniscoid' Polydesmida. 32. *Amphitomeus attemsi* (Schubart, 1934) (Oniscodesmidae), left gonopod, caudal view. 33 & 34. *Elassystremma* sp. (Ammodesmidae), entire animal and ventral side of male body segment 7, lateral and ventral views respectively. 35 & 36. *Hyperothrix orophura* Attems, 1900 (?Pyrgodesmidae), anterior body portion and left gonopod, lateral and caudal views, respectively. [32 after Golovatch *et al.* (2002) (reprinted courtesy of *Arthropoda Selecta*); 33 & 34 after Van den Spiegel (in prep.) (reprinted courtesy of the Royal Museum for Central Africa, Nadine Van Noppen del.); 35 & 36 after Attems (1900). Scale bar 0.1 mm (32), others reproduced not to scale.]

view; the gonopods *in situ* are strongly sunken, flattened dorsoventrally, rather poorly exposed in lateral view, and the coxae are rather strongly hypertrophied (Fig. 36), completely hiding the relatively stout and complex telopodites inside a gonocoel; a solenomere branch is evident (Fig. 36).

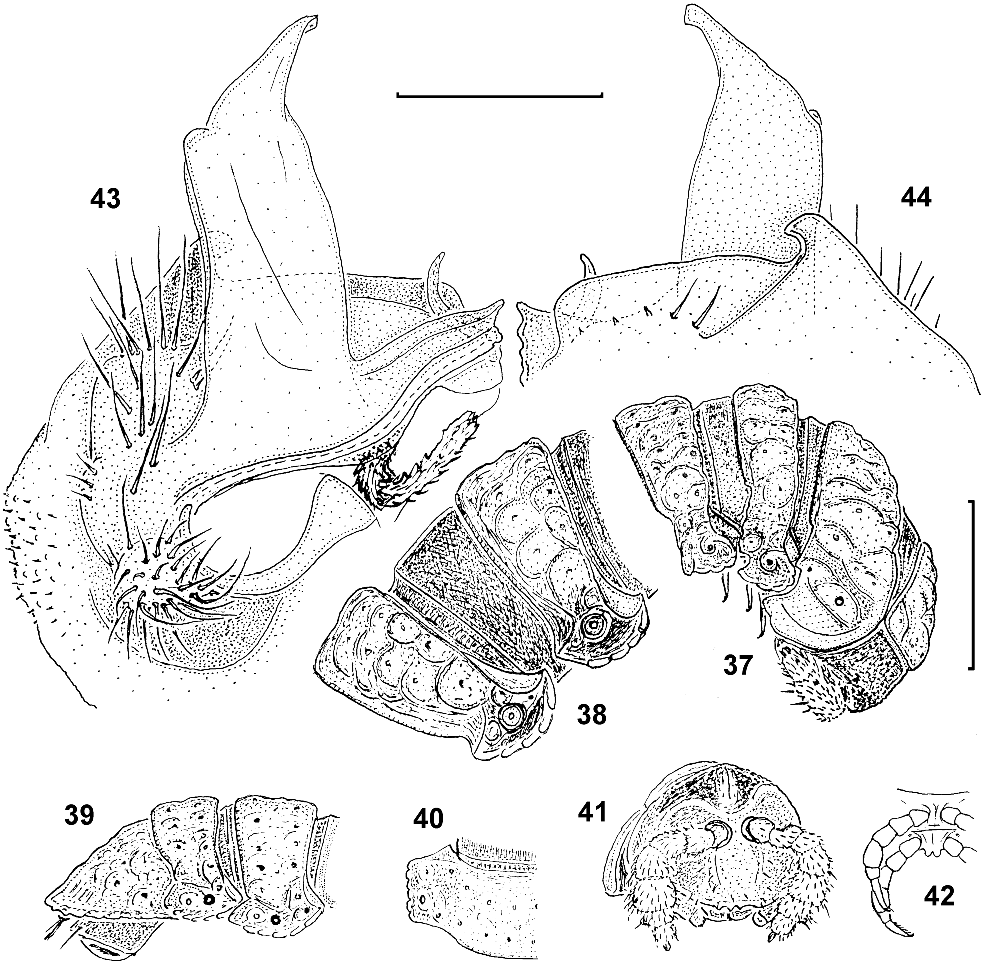
Volvation can definitely be postulated as incomplete. The overlap is typical, starting from paraterga 4 onwards, i.e. as in *Elassystremma* except for the enlarged tergum 2 lacking any schism-like structures.

Direct field observations (Mesibov 2002) confirmed very poor volvatory capacities in still another enigmatic genus, ***Asphalidesmus*** Silvestri, 1910, from Tasmania (Figs 45, 46). Both known species are small (5–6 mm long), showing a roughened vertex, an enlarged, cap-shaped, anteriorly non-lobulated collum which largely conceals the head from above (Fig. 46); metatergum 2 is rather strongly enlarged and is devoid of a schism but, as usual, it supports the anterolateral part of tergum 3; each metatergum subsequent to the second has numerous (5–6) transverse rows of uniform, low, setigerous tubercles; the ozopore formula is (nearly) normal, and each ozopore opens flush on the surface dorsal to a lobulated edge of the paratergum; the paraterga are strongly declined ventrad, yet they fail to reach the level of the sterna; antennomere 6 is the longest and largest (Fig. 46); the limbus is bacillary, upright, and prominent; the telson is ‘polydesmoid’, and the epiproct is conical, and readily visible from above (Fig. 45); the legs are rather stout, especially so in males, but otherwise unmodified (Fig. 46) (Mesibov 2002).

The volvation is remarkable in being devoid of any switch to a typical pattern. Instead it remains the same from tergum 3 onwards, whence the anterior part of the paratergum rests on top of, not beneath, the caudolateral part of the previous paratergum. The overlap is thus simple, apparently plesiomorphic (Fig. 45), and totally different from the more specialised patterns observed in more readily or truly volvatory Polydesmida.

The genus *Asphalidesmus* has provisionally been referred to Haplodesmidae (Mesibov 2002). Indeed, superficially these animals look very much like true haplo- or pyrgodesmids, or *Hyperothrix*. However, the genitalic structure of *Asphalidesmus* is quite characteristic of that of Dalodesmidea, Dalodesmoidea, but maybe not of Dalodesmidae, because the sphaeriotrichomes typical of dalodesmids are missing. As in all other Dalodesmoidea so exemplary of the Southern Hemisphere, the gonopod aperture is ovoid, relatively small, and fully containing and concealing the small, medially fused, contiguous gonocoxae crowned with suberect, distally 2-branched, simple, medially contiguous but not fused telopodites, with hypertrophied prefemoral parts (Fig. 46). An allocation of *Asphalidesmus* to Vaalogonopodidae, a small Southern African dalodesmoid group comprising four genera (of which only three are described, cf. Hoffman 1982*b*) likewise devoid of sphaerotrichomes, is not likely. Indeed, in contrast to Dalodesmidae, Vaalogonopodidae are rather pyrgodesmid-like in appearance, and all are medium-sized (10–20 mm long). Their hypertrophied, anteriorly lobed or scalloped collum conceals the head from above; the metatergal tuberculation is regular and somewhat differentiated; some ozopores are borne on porosteles placed at the lateral edge; the paraterga are relatively small and modestly declined ventrad and lobed laterally; the telson is strongly flattened dorsoventrally; and the gonopod coxae are somewhat better separated etc. (Verhoeff 1940; Schubart 1956). *Asphalidesmus* is distinguished by the collum and tergum 2 being relatively modestly developed; the paraterga are very strong and prominently declined ventrad; the ozopores open inside flat craters located far off the paratergal lateral edge, and are never borne on porosteles; the telson is rather ‘polydesmoid’, the epiproct is subcylindrical, not flattened; the metatergal tuberculation is dense, uniform, setigerous; and the gonopod coxae as well as the telopodites are virtually contiguous medially, etc. (Mesibov 2002).

In general, as the classification of Dalodesmidea is perhaps the most controversial within the entire order Polydesmida (cf. Hoffman 1980; Simonsen 1990), no family placement of *Asphalidesmus* is attempted here as this would apparently be premature.



Figs 37–44. *Agnurodesmus siolii* Golovatch, 2001 (Cyrtodesmidae). 37–39. Anterior body end, body segments 9 and 10, and caudal body end, lateral view. 40: Left side of metatergum 10, dorsal view. 41: Head, subfrontal view. 42: Midbody legs, ventral view. 43 & 44. Right gonopod, submesal and sublateral views, respectively. [All after Golovatch (2001) (reprinted courtesy of *Amazoniana*). Scale bars 0.4 mm (37–42) and 0.1 mm (43 & 44).]

DISCUSSION

As it follows from the above, and in accordance with earlier views (e.g. Hoffman 1977 1982*b* 1990; Hoffman & Howell 1981; Simonsen 1990, etc.), volvation among Polydesmida must have arisen independently several times. Even within individual lineages like Sphaeriodesmidae or Cyrtodesmidae, there are examples of evolutionary change in volvation modes. The progression is clear-cut among Sphaeriodesmidae, with the non-volvatory *Proeilodesmus mecistonyx* being apparently very close to the stem condition. Furthermore, the still not so strictly fixed hypertrophy or differentiation of certain postcollar terga in this family reinforces the above assumption.

In contrast, the situation concerning *Agnurodesmus* seems more ambiguous. This is an imperfectly volvatory genus of Cyrtodesmidae, but in virtually any other respect is definitely among the most advanced members of the family. Although a partial reversal from a volvatory condition that might have been characteristic of the ancestor of *Agnurodesmus* cannot be ruled out, until otherwise documented I am inclined to believe its imperfect volvation mode is a plesiomorphy associated with the still not too strongly enlarged paraterga. The apparently also imperfectly volvatory (= plesiomorphic) *Cyrtodesmus bicolor* is another example of the same progression trend.

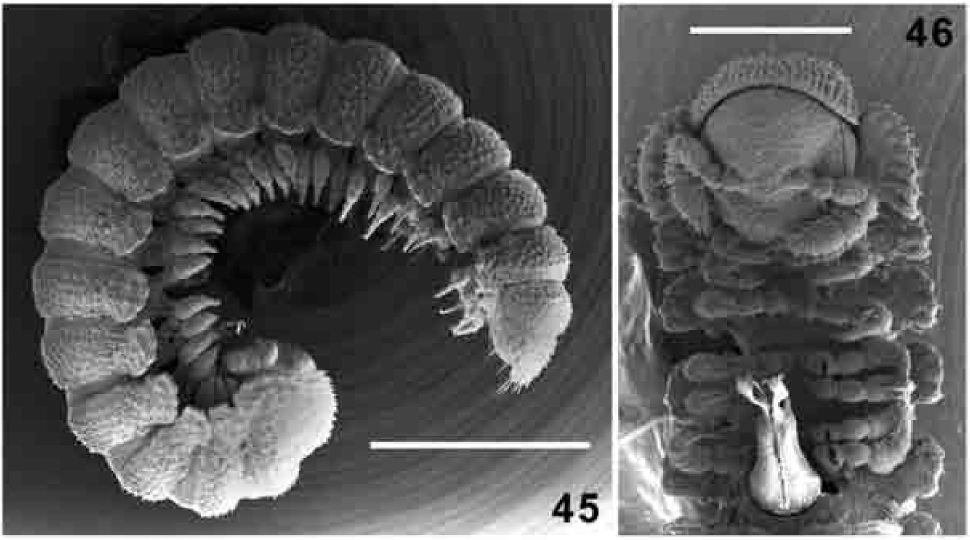
Even within a fully volvatory group such as Oniscodesmidae, there is certain variation in conglobation modes. This situation somewhat resembles that in Glomerida (Oniscomorpha), where two rather closely related genera, *Strasseria* Verhoeff, 1929 and *Trachysphaera* Heller, 1858, also differ in the mechanisms of volvation (Strasser 1971). Simonsen's (1990) opinion that, due to the retained metatergal tuberculation, *Crypturodesmus* is more basal compared to the remaining oniscodesmid genera, seems highly questionable (Golovatch *et al.* 2002) because it contradicts certain morphological evidence (hidden telson, complex gonopods, etc.). Also biogeographically (peripheral, southernmost occurrences), this genus is rather disjunct. However, although it appears impossible to unequivocally state which of the conglobation modes, the *Amphitomeus* or the *Crypturodesmus* one, is more primitive, based on an analogy with *Agnurodesmus*, I am inclined to consider the *Amphitomeus* mechanism as being more elaborate and advanced, with a deep incision-like schism, a greater hyposchism, and narrower ends of the subvertical paraterga (Fig. 28) attesting to that.

Even more problematic is Simonsen's (1990) differences in the shape of the enlarged paraterga 2, to demonstrate parallel evolution in the volvatory members of his superfamilies Oniscodesmoidea and Pyrgodesmoidea. Eventually, one may find the typical, roundly spatuliform paratergum 2 in any of the 'oniscoid' polydesmidean families, with or without a flattened midtergal region. Occasionally there are deviations as in *Agnurodesmus* (Cyrtodesmidae) (Fig. 37), *Detodesmus* (Oniscodesmidae, with strongly elevated anterior and lateral margins coupled with a narrowed and depressed midtergal region), *Hyperothrix* (Fig. 35) or *Campodesmus* (Fig. 8), but the mainstream structure is clearly the same (cf. Figs 7, 12, 17, 20, 22, 27, 33).

Simonsen (1990) also incorrectly opposed the tergal limbus of Doratodesmidae to that of his Pyrgodesmoidea, since among both groups nearly any kind of spatuliform denticles can be present, and the length of the denticles or flattened bacilli also varies with position on the body. Similarly, it appears wrong to discriminate between the legs of Ammodesmidae and Pyrgodesmidae, because the tarsus is relatively slender compared to the tibia not only in both these groups, but also at least in *Hyperothrix*, Cyrtodesmidae and Oniscodesmidae. Treating the Pyrgodesmidae as incapable of volvation is generally correct, but a clear trend toward rolling up, however deficient, observed in several genera of this family cannot be disregarded (see below). In short, too many of the generalisations ventured by Simonsen (1990) using limited material appear groundless or at least questionable.

On the other hand, the lack of a distinct limbus in Oniscodesmidae and probably also in *Dorsoporus* seems to be a valid character, an apparent (syn)apomorphy defining the group together with such traits as the relatively small, subglobose gonopod coxae, and suberect telopodites with particularly prominent prefemoral parts.

Given the new evidence above, though based on the anatomy of the genus *Elassystremma* alone, the choice between Hoffman's (1980 1982*b*) allocation of



Figs 45 & 46. *Asphalidesmus leae* Silvestri, 1910 (Dalodesmoidea). 45. Entire male body, lateral view. 46. Anterior male body end, ventral view. [Both after Mesibov (2002) (reprinted courtesy of the Museum of Victoria). Scale bars 1.0 mm and 0.5 mm, respectively.]

Ammodesmidae within the superfamily Oniscodesmoidea, and Simonsen's (1990) placement within the Pyrgodesmoidea, clearly favours the latter option. The presence of a distinct bacilli- to lobuliferous limbus coupled with the normally highly prominent and exposed gonopod coxae, and a deep gonocoel for the accommodation of relatively small but suberect telopodites, strongly suggest close affinities between ammodesmids and pyrgodesmids.

The same concerns *Hyperothrix*, a taxon definitely belonging in Pyrgodesmoidea as well. Hoffman's (1982*a*) presumed closer relationships of this genus with Doratodesmidae must be rejected because both numerous external traits and, above all, the gonopod conformation appear to be too disparate. However, a family placement of *Hyperothrix* is still problematic as it fully fits none of the families of Pyrgodesmoidea as currently defined. Evolutionarily, this genus seems intermediate between Pyrgodesmidae and Ammodesmidae, yet clearly nearer to or even a true member of the former family in the broad sense. With the description of further Ammodesmidae, a group too poorly known and apparently under-collected because of the extremely small size and mimetism of its species (Cook 1896), some further, hopefully clearer links can be expected to emerge.

In addition, among unquestioned extant Pyrgodesmidae there are several genera like the monobasic neotropical *Arionus* Chamberlin, 1923 and *Stenitus* Chamberlin, 1923, or the afrotropical *Hercodesmus* Cook, 1896, in which paraterga 2 are relatively strongly enlarged while the collum is sometimes relatively small. This is a condition readily reminiscent of *Hyperothrix*. None of these genera can be considered as truly volvatory either, instead rather representing a trend in the superfamily Pyrgodesmoidea.

As mentioned earlier, a body conformation superficially very strongly resembling that of some haplodesmids, *Hyperothrix*, *Arionus* and the remaining few imperfectly volvatory pyrgodesmoids with enlarged metaterga 2, is also observed in *Asphalidesmus*.

However, as the genus *Asphalidesmus* seems exceptional among Dalodesmoidea while its family-level relations are still uncertain, no clear-cut trend to volvation is more obvious in Dalodesmoidea as opposed to Pyrgodesmoidea.

The patterns of volvation in ‘oniscoid’ Diplopoda attest to the widely accepted parallelisms in polydesmidan evolution. Generally, enrolling the body among Chelodesmidea tends to entail no or relatively little differentiation of tergum 2 compared to the subsequent terga, whereas among the Polydesmidea it is only a hypertrophied tergum 2 that is adapted to conglobation. However, an enlarged tergum 2 is a prerequisite, but apparently not the only condition for the development of volvation. This is clear from certain Haplodesmidae, several pyrgodesmoids like *Hyperothrix, Arionus* etc., or the dalodesmoid *Asphalidesmus*, which are all incapable of enrolling because of the apparently too narrow and small paraterga failing to surpass the level of the sterna ventrally.

The extant ‘oniscoid’ families of Chelodesmidea appear to be fewer than in Polydesmidea, with some members in the two families concerned still showing conditions close enough to the presumed stem. Such are the entirely non-volvatory *Proeilodesmus* and the incompletely volvatory *Campodesmus*. In contrast, ‘oniscoid’ Polydesmidea appear to be far more diverse and widespread. The incision/lobulation patterns of their hypertrophied, usually roundly scapuliform paraterga 2, coupled with often particular volvation mechanisms, seem to largely characterise genera rather than families. Among the ‘oniscoid’ polydesmideans, the few Cyrtodesmidae incapable of complete volvation appear to be the oligotypic genus *Agnurodesmus* and the species *C. bicolor*. The same concerns *Hyperothrix* (?Pyrgodesmidae) as well as all true Pyrgodesmidae, including such superficially rather ‘oniscoid’ genera like *Arionus, Hercodesmus,* and *Stenitus*. A very similar situation is observed in *Asphalidesmus*, apparently the only genus of Dalodesmidea inclined to volvation, however imperfect.

Conglobation among diplopods tends to concern smaller and cryptic species with relatively few body segments (a little over 20 at most), declined paraterga, often a mimetic coloration, hardened (except for cave-dwelling forms) teguments, at least one strongly enlarged postcollar tergum (usually 2nd, with an apparently correlated size reduction of the collum), commonly more or less reduced ozopores and telson, and normally relatively short and poorly separated legs and antennae (cf. Simonsen 1990). Each or even several of these traits can readily occur in some non-volvatory lineages as well, but the more profound and numerous the above modifications, the more perfect the volvation mechanism and the conglobation achieved. The patterns of volvation seem to generally reflect the generic level only, with numerous parallelisms.

The distribution of volvation among Polydesmida, and amongst Diplopoda as a whole, shows not only taxonomic but also clear geographical patterns. Thus, the only fully volvatory group which is largely extratropical in distribution is the order Glomerida, while the bulk of ‘oniscoid’ millipede diversity is definitely confined to tropical/subtropical regions. Most of the polydesmidan groups capable of conglobation tend to be strictly vicariant, only Oniscodesmidae (with *Dorsoporus*) and Cyrtodesmidae showing a considerable range overlap in Central and northern South America. This confirms multiple parallel and successional developments among ‘oniscoid’ Polydesmida, most likely with vicariance involved.

What seems noteworthy is that none of the ‘Juliformia’ can volvate, apparently because the maximum number of segments capable of doing this seems to be around 20. Any more and it gets ‘too crowded’, as it were.

The fewer segments, the better appears to be the conglobation potential in general. To make a true sphere, like in the Oniscomorpha, a lot of tergal overlap is required when the animal is unrolled and crawling, because when it rolls up, the exposed dorsal surface becomes far (>2 times) greater. The more this is true, the smaller (lengthwise) the sterna have to become.

Truly large Polydesmida like some Chelodesmidae or Platyrhacidae seem to have never volvated. Maybe 20 body segments can compact, structurally, only in relatively small forms, while to get a large oniscomorph like *Sphaeropoeus hercules* Brandt, 1833 (Sphaerotheriida), which is the size of a golf ball when rolled up, only some 13 segments are allowable. Similarly, the often large and conspicuously spinose species of the fossil, Palaeozoic, oniscomorph order Amynilispedida, comprised 14 body segments only. Like some volvatory woodlice (Oniscidea, Isopoda) (cf. Lawrence 1953), certain Glomerida display a tendency toward size reduction of their caudal terga. Thus, the penultimate tergite in *Trachysphaera* is so strongly reduced that it remains visible as a thin ribbon in lateral view only.

The concentration of volvation in the New World tropics is interesting. Overall, the global expression of this ability in polydesmidans seems to complement the distribution of Oniscomorpha, with few and trivial overlaps only (Hoffman, in litt.).

It still remains to be investigated whether the patterns of volvation among ‘oniscoid’ Polydesmida change during ontogeny, and may also involve some kind of lock mechanism, both these traits long observed amongst Oniscomorpha.

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